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Update on the Flower Associations of Southern African Masarinae with Notes on the Nesting of *Masarina strucki* Gess and *Celonites gariepensis* Gess (Hymenoptera: Vespidae: Masarinae)

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Abstract.—Flower visiting records are presented for seven newly described species of Masarinae from the Richtersveld and for *Masarina strucki* Gess. The potential of these wasps as pollinators is discussed. *Celonites gariepensis* Gess and *Masarina peliostomi* Gess are associated with *Peliostomum* and the former, at least, with *Aptosimum* (Scrophulariaceae), a preference shared with four other species of *Celonites*. *Masarina tylecodoni* Gess appears to be restricted to *Tylecodon hallii* (Tölken) Tölken (Crassulaceae) and is apparently the first recorded insect visitor to a *Tylecodon* species. *Jugurtia codoni* Gess is an abundant visitor to *Codon royenii* L. of the family Hydrophyllaceae, one of the preferred forage plant families of the North American masarines but otherwise not known to be visited by masarines. Records for *Masarina strucki* from a wide range of localities confirm its, for a masarine, unusual association with *Hermannia* spp. (Sterculiaceae). In the Richtersveld *Zygophyllum* spp. (Zygophyllaceae) were being visited, though not apparently favoured, by *Ceramius brevitarsis* Gess, two species of *Jugurtia*, *J. codoni* Gess and *J. koeroegabensis* Gess, and *Masarina mixtoides* Gess. These records are of interest as *Zygophyllum* has only otherwise been shown to attract one other species of Masarinae, a *Quartinioides* species, in the Central Namib Desert. Some aspects of the nesting of *C. gariepensis*, which constructs aerial mud cells, and of *M. strucki*, which nests in the ground, are presented and discussed.

Gess (S.K. 1996) presented a synthesis of the available data on the nesting and flower visiting of the Masarinae in southern Africa. Recent fieldwork in southwestern southern Africa, most notably in the previously under collected Richtersveld National Park in the extreme north of Namaqualand (Fig. 1) (16–24.ix.1995 and 5–18.ix.1996), has resulted in the discovery of new species, additional flower associations of particular interest, and a nest each of *Masarina strucki* Gess and *Celonites gariepensis* Gess. Descriptions of the new species are given in Gess (F.W. 1997) and the flower visiting and nesting data are presented and discussed in the present paper.

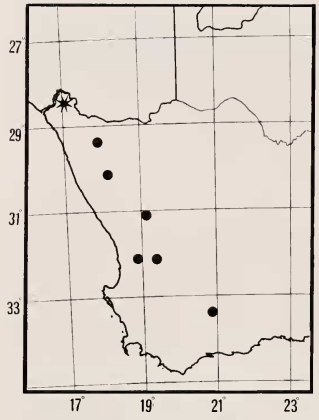
Some other masarines collected in the Richtersveld National Park, all extending the known distributions for the species, are: *Ceramius cerceriformis* Saussure, four species of *Jugurtia*, *J. braunsi* (Schulthess), *J. braunsiella* (Schulthess), *J. calcarata* Richards, and *J. duplicata* Richards, two species of *Celonites*, *C. clypeatus* Richards and *C. peliostomi* Gess. Flower visiting records for these species of *Jugurtia* and *Celonites* confirm previously recorded flower family choices (Gess, S.K. 1996).

Celonites Latreille

Celonites gariepensis Gess

Distribution.—*Celonites gariepensis* Gess has been recorded from only the Richtersveld National Park in northern Namaqualand (Gess, F.W. 1997).

Flower visiting.—On the Koeroegabvlakte (28.11S, 17.03E) (Figs. 2–5) *C. gariepensis* females and males were foraging only on flowers of a species of *Peliostomum* (Scrophulariaceae), together with *Celonites clypeatus* Brauns, *Celonites peliostomi* Gess (Fig. 6) and *Masarina peliostomi* Gess (Fig.



Figs. 1. Map of southwestern southern Africa. Dots mark areas from which *Masarina strucki* Gess has been collected. Star marks the position of the Richtersveld National Park.

7), and on *Aptosimum spinescens* (Thunb.) Weber (Scrophulariaceae), together with *C. peliostomi*. The plants were growing on the banks of a dry gravelly drainage channel (Figs. 4 and 5). *Celonites clypeatus* and *C. peliostomi* together with *Celonites andrei* Brauns and *Celonites tumidiscutellatus* Gess have previously been shown to be associated solely with *Peliostomum* and *Aptosimum* (Scrophulariaceae). Taking into account in addition size fit and behaviour, these species are considered to be, in the areas where they occur, the most dependable potential pollinators of the species which they visit (Gess and Gess 1989; Gess, S.K. 1996; Gess, F.W. 1997). Being of similar size and behaviour, *C. gariepensis* is considered to be an additional potential pollinator of the present two species of *Peliostomum* and *Aptosimum* visited by it in the Richtersveld.

The specific identity of the *Peliostomum* species was not established. The much branched, rounded shrublets were up to 30 cm in height. The thicker stems, like those of *Peliostomum leucorrhizum* E. Mey. ex Benth., were strikingly pale. On the other hand the flowers were, in shape and markings, similar to those of *Peliostomum virgatum* E. Mey. ex Benth. (compare Fig. 7 and Gess, S.K. 1996, Fig. 24) not to those of *P. leucorrhizum* in which the narrow basal part of the tube is purple. However, unlike *P. virgatum* but like *P. leucorrhizum* the stems, leaves and flowers were not sticky.

Nesting area.—Only one nest of *C. gariepensis* was located. This nest was sited on the underside of a jutting edge in a rock crevice near the base of a slope in Paradise Kloof (28.19S, 17.01E) (Figs. 8–10).

Provision.—The provision was pale grey, very moist but, having a papillate surface (Fig. 12), barely touched the cell walls.

Description of nest.—The nest, which was still under construction, consisted of three earthen cells attached longitudinally to their horizontal rock substrate. Two cells were complete and attached to each other longitudinally and the third incomplete cell was being constructed with its closed end abutting the seal of one of the completed cells. The cells were 9 mm long and 4 mm wide at mid-length. Characteristic of *Celonites* cells is the distinct "fish scale" pattern on the outer surface of the constructed earthen-cell (Fig. 11) and the seal constructed just inside the cell opening (Gess, S.K. 1996). Like the cells of *Celonites abbreviatus* (Villers) described by Bellman (1984) the cell walls were incomplete, the cells being open to the substrate.

Nest construction.—As *C. gariepensis* was not found at water it is likely that, like other *Celonites* species, it does not use water in cell construction. The hard brittle nature of the cell walls suggests that nectar is probably the bonding agent as has been suggested for other *Celonites* species (Gess, S.K. 1996).

Figs. 2–5. Koeroegabvlakte, Richtersveld National Park. 2, looking north east from a hill, the *Masarina tylecodoni* Gess site, on the west flank of the flats. 3, the flats. 4, dry drainage channel, *Zygophyllum prismatocarpum* E. Mey ex Sond (Zygophyllaceae) in foreground. 5, Dry drainage channel to the west of the flats from above.

Ceramius Latreille

Ceramius brevitarsis Gess

Distribution.—*Ceramius brevitarsis* Gess has been recorded from only the Richtersveld National Park in northern Namaqualand (Gess, F.W. 1997). It belongs in *Ceramius* Group 2A together with *Ceramius cerceriformis* Saussure and *Ceramius perinqueyi* Brauns. It is the most northern Namaqualand species of *Ceramius* having been found in the hills in the north of the Richtersveld National Park. The only other species of *Ceramius* recorded from the Park as yet is the relatively widely distributed (Gess, S.K. 1996) *C. cerceriformis* which was recorded from the hills to the

Figs. 6 and 7. *Peliostomum* sp. (Scrophulariaceae). 6, *Celonites peliostomi* Gess preparing to enter flower. 7, *Masarina peliostomi* Gess entering flower (length of flower approximately 20 mm).

south. To the north of the Richtersveld National Park there is a surprising hiatus in the known distribution of *Ceramius*, no species having been recorded between there and northern Namibia whence a single species from Group 4, *Ceramius damarinus* Turner, was described by Turner (1935) from females and a male from Ongandjera (1923) and a male from Kamanyab (1925), part of material collected by the staff of the South African Museum (Gess, F.W. 1965). Recently this species was recorded flying abundantly 10.3 km NW on the road from Okaukuejo to Okondeka, 3.iv.1996, by D.W. and G.T. Gess. A sample of twelve females was taken.

Water visiting.—*C. brevitarsis* was found to be abundant at a trickle of water crossing the road in a rocky pass (28.10S, 17.02E) immediately to the north of Koeroegabvlakte. Whilst imbibing water the wasps stood on wet sand or rock at the edge of the water. One further female was observed imbibing water from the edge of an isolated pool of water in a hollow on a steeply sloping rock. In this instance the surface on which the wasp stood was dry, indicating that water is imbibed directly from the pool and not from wet sand as has been observed for *Ceramius bicolor* (Thunberg) (Gess, S.K. 1996) and *Ceramius socius* Turner (Gess and Gess 1986). In no case did one of these wasps alight on the water surface.

Flower visiting.—All plants in flower in the vicinity of the water were sampled for flower visitors throughout the day, however, only one female and one male of *C. brevitarsis* were taken. Both were visiting the small cream flowers of *Zygophyllum prismatocarpum* E. Mey. ex Sond. (Zygophyllaceae). This is the first record of *Ceramius* visiting flowers of Zygophyllaceae. The records are, however, too few for an association to be suggested as instances of casual visiting of flowers other than those preferred has occasionally been recorded for some species of *Ceramius* (Gess, S.K. 1996). Aizoaceae: Mesembryanthema would be the expected plant taxon to be favoured by *C. brevitarsis*, it being a member of Group 2A and there being consistency of flower family choice within *Ceramius* species groups in southern Africa (Gess, S.K. 1996).

Jugurtia de Saussure

Jugurtia codoni Gess

Distribution.—*Jugurtia codoni* Gess has been recorded from only the Richtersveld National Park in northern Namaqualand (Gess, F.W. 1997).

Figs. 8–12. Paradise Kloof, Richtersveld National Park. 8, Approach to kloof. 9, Nesting site of *Celonites gariepensis* Gess marked with arrow. 10, Nest of *C. gariepensis* on underside of jutting edge in rock crevice (outer cell broken during capture of builder). 11, Cell of *C. gariepensis*. 12, Cell of *C. gariepensis* opened to show papillate provision mass and position of egg.

Water visiting.—Two females of *J. codoni* were collected at the edge of a pool of water in Paradise Kloof. This suggests that it is probable that *J. codoni*, like the other species of *Jugurtia* for which nesting is known, uses water in nest construction.

Flower visiting.—Females of *J. codoni* were found foraging abundantly on the flowers of the spiny, metre high herb *Codon royenii* L. (Hydrophyllaceae) growing in the gravelly bed of a dry watercourse, where it emerged from the hills before crossing the Koeroegabvlakte (Fig. 5). The flowers of *C. royenii* are 35 mm high, erect and campanulate (Figs. 13–15). The many lobed corolla is white. There are 10–12 stamens. The filaments are attached to the corolla tube about 5 mm from the base and are closely adpressed so that they close off the base of the flower (Fig. 15) presumably protecting the nectar from evaporation. *Jugurtia codoni*, when visiting a flower, alights on the outwardly curved corolla lobes and, when preparing to imbibe nec-

Figs. 13 and 14. *Codon royenii* L. (Hydrophyllaceae). 13, *Jugurtia codoni* Gess imbibing nectar. 14, *J. codoni* collecting pollen.

tar, walks down the side of the flower (Fig. 13) and inserts its long tongue between the filaments. When collecting pollen, the wasp either reaches over from the corolla or moves across onto a filament and ingests the pollen directly from the anther (Fig. 14). Although apparently preferring *C. royenii*, *J. codoni* was found less commonly visiting the flowers of *P. leucorrhizum* (Scrophulariaceae) and of *Hermbstaedtia glauca* (Wendl.) Reichb. ex Steud. (Amaranthaceae). At other sites in the Park it was found uncommonly visiting flowers of *Zygophyllum meyeri* Sond. (Zygophyllaceae), *Senecio arenarius* Thunb. (Asteraceae) and *Pelargonium klinghardtense* Knuth (Geraniaceae).

Due to the smallness in size of *J. codoni* compared with *Codon royenii* it is possible for *J. codoni* when obtaining nectar to enter and leave the flowers without coming into contact with either the anthers or the stigmas and to collect pollen from the anthers without coming into contact with the stigmas. It is therefore probable that, whereas *C. royenii* is clearly an important forage plant for *J. codoni*, *J. codoni* is not a potential pollinator of *C. royenii* but is rather a pollen and nectar thief. A more likely potential pollinator is the relatively large bee *Xylocopa lugubris* Gerstaecker (Apidae: Xylocopinae) which, although it is a less common visitor and not restricted to *Codon*, in behaviour and fit is ideally suited to act as a pollinator.

Jugurtia koeroegabensis Gess

Distribution.—*Jugurtia koeroegabensis* Gess has been recorded from only the Richtersveld National Park in northern Namaqualand (Gess, F.W. 1997).

Flower visiting.—Only seven females of *J. koeroegabensis* were collected from flowers. On the banks of a dry watercourse crossing the Koeroegabvlakte (28.11S, 17.03E) (Figs. 2–5) two females were taken from the small cream flowers of *Zygophyllum prismatocarpum* E. Mey. ex Sond. (Zygophyllaceae) and one female was taken from a yellow rayed capitulum of *Osteospermum* sp. (Asteraceae). At Pootjiespram (20.05S, 16.57E), in a broad sandy drainage area, four females were taken visiting flowers, one from the yellow petalled flowers of *Cleome paxii* (Schinz) Gilg. & Benth. (Capparaceae), one from the flowers of *Peliostomum leucorrhizum* (Scrophulariaceae) and two from the green and brown flowers of *Ferraria* cf *divaricata* Sweet (Iridaceae). These records are too

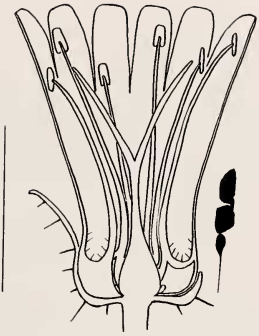


Fig. 15. *Codon royenii* L. (Hydrophyllaceae), Diagrammatic representation of flower cut longitudinally and of *Jugurtia codoni* Gess (wings and legs omitted).

few to establish a particular preference, however, it is clear that *J. koeroegabensis* is not restricted to visiting flowers of a single plant family.

Masarina Richards

Masarina mixtoides Gess

Distribution.—*Masarina mixtoides* Gess has been recorded from only the Richtersveld National Park in northern Namaqualand (Gess, F.W. 1997).

Flower visiting.—*Masarina mixtoides* is not restricted to a single family of plants. At a site 1.5 km from the Helskloof Gate (28.18S, 16.57E), the abundant white flowers of an isolated plant of *Pelargonium klinghardtense* Knuth (Geraniaceae) growing on the edge of a dry, stoney drainage channel on a hillside were clearly attractive to this wasp, a sample of 15 females and one male having been taken in under an hour. However, on the Koeroegabvlakte, where flowers associated with a dry, gravelly drainage channel crossing the flats (Figs. 2–5) were sampled, three females were taken from the small cream flowers of lax, shrubby *Zygophyllum prismatocarpum* (Zygophyllaceae) (Fig. 4), and four from the larger yellow flowers of compact, shrubby *Zygophyllum meyeri*. In addition one female was collected from the flowers of a species of *Wahlenbergia* (Campanulaceae) and one from a yellow rayed capitulum of Asteraceae.

Masarina peliostomi Gess

Distribution.—*Masarina peliostomi* has been recorded from only the Richtersveld National Park (Gess, F.W. 1997).

Flower visiting.—Both females and males of *M. peliostomi* were foraging abundantly on the flowers of *Peliostomum leucorrhizum* (Scrophulariaceae) (Fig. 7) growing along the banks of the upper reaches of a dry watercourse crossing the Koeroegabvlakte (Figs. 2–5). This is the first record of an association between a species of *Masarina* and a species of *Peliostomum*. However, five species of *Celonites* are known to be associated with plants of this genus (see above). *Masarina peliostomi* being of similar size and behaviour to the *Celonites* species should, like them, be considered a potential pollinator of *Peliostomum* in the Richtersveld. Although not collected from flowers of *Aptosimum spinescens*, which was growing further down the watercourse, it is probable that *M. peliostomi* would visit these flowers.

Masarina strucki Gess

Distribution.—*Masarina strucki* has been recorded from Namaqualand (Goegap Nature Reserve, Springbok and the western side of the Kamiesberg), the Olifants River Valley to the south (east bank of the Clanwilliam Dam), immediately east of the Western Escarpment (Skuinshoogte Pass between Nieuwoudtville and Louriestontein and Biedouw Valley in the Cederberg) and in the western Little Karoo (Ladismith) (Gess, F.W. 1997).

Flower visiting.—The first record was for a single female collected by Michael Struck, 20.viii.1985, visiting the yellow

flowers of *Hermannia disermifolia* Jacq. of the subgenus *Hermannia* (Sterculiaceae) in Goegap Nature Reserve (formerly Hester Malan Nature Reserve) in the Springbok district, Namaqualand. An intensive search by the Gesses for this masarine during six subsequent spring visits to Namaqualand yielded only one further female, from the same locality (10–12.x.1988, F.W. and S.K. Gess), until spring 1994 when they found females and males relatively abundant in association with *H. disermifolia* in the Goegap Nature Reserve (primarily at 29.37S, 17.59E) (3-8.x.1994, F.W. and S.K. Gess) and at Bakleikraal (30.13S, 18.03E) in the Kamiesberg (9-11.x.1994, F.W. and S.K. Gess) (Figs. 16 and 17). The following spring, 1995, they again found females and males at the Kamiesberg site (28.ix.1995, F.W., S.K. and R.W. Gess) but none were found at the Goegap site. The sites in the Goegap Nature Reserve and the Kamiesberg are level sandy areas at the base of rocky outcrops, in which *H. disermifolia* is the dominant plant.

In the Olifants River Valley on the east bank of the Clanwilliam Dam, 19.2 km south of the caravan park (32.17S, 18.56/7E) *M. strucki* was found by Robert Gess foraging on an orange flowered species of *Hermannia* subgenus *Mahernia* (3 females, 5.x.1995, F.W., S.K. and R.W. Gess) growing in sandy soil at the foot of a rocky slope.

At the Skuinshoogte Pass site (31.16S, 19.08E) only two females were collected (23-30.ix.1994, F.W. and S.K. Gess), one on the ground in a dry river bed and the other on the ground beneath a shrublet of a yellow flowered species of *Hermannia* subgenus *Hermannia*.

In the western Little Karoo two samples have been taken in the Ladismith district, one at Buffelspoort (3320BD) (3 females, 14.viii.1995, V.B. Whitehead) on a yellow flowered shrubby *Hermannia* sp. and the other 6 km from Ladismith on the road to Barrydale (3 females, 21.viii.1995, F.W. and S.K. Gess) visiting yellow flowers of *Hermannia vestita* Thunb. of the subgenus *Hermannia* growing in level ground on the roadside halfway up a rocky slope.

It seems probable that *M. strucki* is always associated with *Hermannia* spp. as careful collecting by the Gesses from a wide range of flowering plants both in the vicinity of its collection sites and further afield has been undertaken. It also seems to be of note that the *Hermannia* plants with which it has been found have all been associated with rocky hill slopes.

The flowers of the *Hermannia* spp. recorded as being visited by *M. strucki* are all "bell-shaped" and 7–10 mm in length. *Masarina strucki*, of which the females are an average length of 7.4 mm and the males 6.6 mm, alights on the side of the downwardly hanging flowers, moves down, and curves around the lip to face upwards into the flower (Fig. 22h). When remaining in this position an individual is apparently ingesting pollen. When the individual enters into the flower leaving only its abdomen exposed it is undoubtedly imbibing nectar. The nectar held in the inrolled bases of the petals will be reached by the wasp's tongue which has an average length of 4.2 mm in the female and 4.0 mm in the male.

As a flower visitor *M. strucki* appears to be restricted to *Hermannia* and therefore to be dependant upon this genus for pollen and nectar. Its distribution is far more limited than that of *Hermannia* and within the areas where it does occur it seems to be restricted to rocky slopes and on these slopes to a limited range of *Hermannia* species. It is, however, not the sole visitor to these species of *Hermannia* (Table 1). Assemblages of visitors to the three species of *Hermannia* subgenus *Hermannia* with which it has been associated are characterized by the presence of, in addition, one or more species of *Anthophora* (*Pyganthophora*) (Apidae: Apinae: Anthophorini) and one or more species of Megachilidae—one or more species of *Plesianthidium*

Figs. 16–18. 16, Nesting area of *Masarina strucki* Gess, Kamiesberg, bushes in the foreground, *Hermannia disermifolia* Jacq. (Sterculiaceae). 17, Flowers of *H. disermifolia* (length of flower approximately 9 mm). 18, Cell of *M. strucki* opened to show papillate provision mass and position of egg.

(*Spinanthidium*) (Megachilidae: Megachilinae: Anthidiini) and/or a species of *Lasioglossum* (Halictidae). Though these bees are therefore also expected visitors to the flowers they are less constant as they are all known to visit in addition flower species of other genera belonging to other plant families occurring in close proximity to the *Hermannia* plants.

Masarina strucki and the bees all visit a considerable number of flowers in succession, and all while visiting flowers in the pollen-presenting stage receive a dusting of pollen which adheres to them. *Masarina strucki* in entering the flowers receives the pollen dorsally and the bees which are all too large to enter receive pollen on their hairy faces. Such pollen would be transferred to receptive stigmas by the wasps and the bees visiting flowers in the receptive phase. All can therefore be considered to be potential pollinators, but where they are present the masarines will be the more dependable.

The species of *Hermannia* subgenus *Mahernia* was sampled on one day only. On this day it was only visited by two masarines, *M. strucki* and *Masarina mixta* Richards. Both can be considered potential pollinators, however, *M. strucki* is more dependable than *M. mixta* which visits in addition flowers of plants of several other families which grow in close proximity to the *Hermannia* plants.

Table 1. Flower visitors to those species of *Hermannia* L. on which *Masarina strucki* Gess is known to forage. Number in brackets indicates the number of plant families in addition to Sterculiaceae which are known to be visited.

subgenus *Hermannia*
Hermannia disermifolia Jacq. and *Hermannia* cf. *disermifolia*
Vespidae: Masarinae
Masarina strucki Gess, Goegap, Kamiesberg, (Skuinshoogte) (0)
Vespidae: Eumeninae apparently hunting
Megachilidae: Megachilinae: Anthidiini
Plesianthidium (*Spinanthidium*) *callescens* (Cockerell), Skuinshoogte (1)
Plesianthidium (*Spinanthidium*) *trachusiforme* (Friese), Goegap (1)
Apidae: Apinae: Anthophorini
Anthophora (*Pyganthophora*) *abrochia* Eardley, Goegap, Kamiesberg (1)
Anthophora (*Pyganthophora*) *diversipes* Friese, Kamiesberg (3)
Anthophora (*Pyganthophora*) *krugeri* Eardley, Goegap (1)
Anthophora (*Pyganthophora*) *schultzei* Freise, Skuinshoogte (2)
Amegilla (*Micramegilla*) *niveata* (Friese), Kamiesberg, Skuinshoogte (16)
Pachymelus peringueyi (Friese) Goegap, Kamiesberg (3)
Apidae: Apinae: Apini
Apis mellifera L. (very many)
Scarabaeidae: Melalonthinae: Hopliini
A single species
Hermannia cf. *cuneifolia* Jacq.
Vespidae: Masarinae
Masarina strucki Gess, Goegap, (Skuinshoogte) (0)
Vespidae: Eumeninae apparently hunting
Halictidae
Lasioglossum sp., Skuinshoogte (?)
Megachilidae: Megachilinae: Anthidiini
Plesianthidium (*Spinanthidium*) *callescens* (Cockerell), Skuinshoogte (1)
Apidae: Apinae: Anthophorini
Anthophora (*Pyganthophora*) *schultzei* Freise, Skuinshoogte (2)
Hermannia vestita Thunb.
Vespidae: Masarinae
Masarina strucki Gess, Ladismith (0)
Halictidae
Lasioglossum sp., Ladismith (?)

Table 1. Continued.

Apidae: Apinae: Anthophorini
Anthophora (*Pyganthophora*) *krugeri* Eardley, Ladismith (1)
Nemestrinidae
Prosoeca sp.
subgenus *Malvernia*
Hermannia sp.
Vespidae: Masarinae
Masarina mixta Richards, Clanwilliam (3)
Masarina strucki Gess, Clanwilliam (0)
Vespidae: Eumeninae apparently hunting

Nesting area.—Unfortunately despite careful search only one nest has been located. This was at the Bakleikraal site in the Kamiesberg (Fig. 16). The nest entrance was between two stones in gently sloping ground in a bare area between the *Hermannia* bushes. The soil was sandy and friable.

Provision.—The provision from the single cell obtained was very moist but jelly-like, pale yellow ochre, and translucent. The longitudinal surface was regularly papillate, each papilla ending in a nipple (Figs. 18 and 19b). At the inner end of the provision was a larger central papilla which supported the egg. The outer end

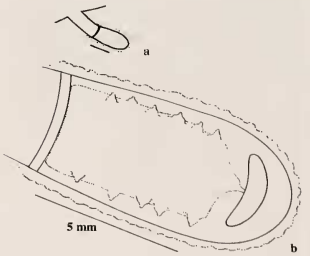


Fig. 19. Diagrammatic representations of longitudinal section of nest and cell, papillate provision mass and egg of *Masarina strucki* Gess.

of the provision was adpressed to the cell closure.

Samples of pollen were taken from the provision and examined microscopically. The pollen was all of one kind, 0.03 mm in diameter, and matched pollen from *H. disermifolia*.

Description of nest.—The single nest investigated consisted of a sloping burrow (3.5 mm in diameter and 6.5 mm in length) terminating in a cell (Fig. 19a). The cell which was rounded at the inner end and sealed with a seal, 0.5 mm in thickness, concave on the outside and convex on the inside, had an inner length of 7.9 mm and an inner diameter of 3.7 mm. The walls of the cell were smoothed on the inside and the surrounding earth was cemented to a depth of 0.5 mm so that the cell could be removed from the surrounding soil as an entity. There was no entrance turret.

Method of construction, oviposition and provisioning.—The nest was discovered after the burrow had been excavated and the cell walls were being smoothed and stabilized. The friable nature of the soil, the lack of any form of turret, the lack of discarded mud pellets, and the nature of the cell walls and seal suggest that excavation of the nest had taken place without the use of water but that some bonding agent other than water had been used for cementing the cell walls and constructing the seal. The extreme hardness of the cell walls akin to those of *Celonites* spp. and the pliable nature of the freshly completed seal suggest the use of nectar.

When observations commenced at 14h56 final smoothing of the cell walls was apparently in progress. The wasp repeatedly moved backwards until half the body length protruded from the entrance and forwards again into the cell. By shining a light into the nest and using a dentist's mirror during the wasp's absence it could be seen that the cell walls were smooth and moist.

At 15h12 the builder, after an absence of eight minutes, returned to the nest and entered it head first. After apparently making an inspection she came out, turned around and reversed into the nest dorsum uppermost, emerged again eight minutes later, and then re-entered facing into the cell. Oviposition had apparently taken place. The egg which was obtained when the nest was later investigated was white, curved, and tapered somewhat towards the ends. It was 2.4 mm in length across the bow and 0.75 mm in diameter at mid-length.

Provisioning then commenced. This took 85 minutes and was apparently accomplished with five loads as, during this phase, the wasp was away from the nest, apparently foraging, for five periods varying from 6–10 minutes and in the nest rotating (an average of four times), apparently depositing the provision, for five periods of 3–13.5 minutes.

Sealing of the cell commenced after an absence from the nest, apparently to collect nectar. Soil for sealing was seen to be taken from the walls of the entrance shaft. At 17h07 work for the day was over. On emerging from the nest the wasp was observed to groom for the first time. She was then away from the nest for seven minutes presumably feeding before settling for the night. On her return to the nest she went in head first, apparently to inspect the nest, and then came out, backed in, groomed her face, and then became still with her head blocking the nest entrance. The following morning she remained still in the same position, apparently sleeping, until 10h37 when she began to stir and look out of her nest. She, however, only left the nest at 10h56. After an absence of 13 minutes she was back in the nest continuing with the cell closure but not rotating as she had been when provisioning. Cell closure was completed by 11h30.

Male behaviour.—Males of *M. strucki* forage together with the females on the flowers of *Hermannia* spp. They were also observed on the ground beneath the *Herman-*

nia bushes. On the second day (whilst nest construction was being observed), before the female emerged from her nest, a male was seen resting on the ground sunning himself about 2 m from the nest. No instances of mating were observed.

Associated insects.—A probable association between *Allocoelia quinquidens* Edney (Chrysididae) and *M. strucki* is noted. Female *A. quinquidens* were present on the ground between the *Hermannia* bushes at the Goegap and the Bovlei sites. Furthermore on the second day of nesting observations one was observed at 11h34 *ca.* 1 m from the nest, at 11h36 *ca.* ½ m from the nest, at 11h39 30 cm from the nest, at 11h46 *ca.* 1 ½ m from the nest and finally at 11h50 entering the nest and leaving it, at 11h52 *ca.* ½ m from the nest, at 12h02 inspecting and entering the nest, at 12h50, 13h34 and 13h50 inspecting the nest.

It is of note that *A. quinquidens* has also been observed by the Gesses inspecting a nest of *Masarina familiaris* Richards between Clanwilliam and Graafwater.

Masarina tylecodoni Gess

Distribution.—*Masarina tylecodoni* has only been recorded from the Richtersveld National Park in northern Namaqualand (Gess, F.W. 1997).

Flower visiting.—Both females and males of *M. tylecodoni* were discovered by Robert Gess to be foraging on the yellow flowers of *Tylecodon hallii* (Tölken) Tölken (Crassulaceae) growing on rocky hills on the west flank of the Koeroegabvlakte (Figs. 2, 5 and 20). This masarine was foraging abundantly, and apparently exclusively, on these flowers. *Tylecodon hallii* was the only species of *Tylecodon* in flower, so it is not known whether the flowers of other species of *Tylecodon* are visited. As nothing is known of the insect visitors to the flowers of *Tylecodon* (G. Williamson pers. comm.) this is of particular interest.

Tylecodon hallii is a compact succulent shrublet which holds aloft an abundance of yellow erect campanulate flowers (Figs. 20 and 21). The flowers are 22 mm in height. The corolla consists of five fused petals. Each of the ten stamens is fused to the corolla just above the "waist" (Fig. 22).

Figs. 20 and 21. 20, Slope of rocky hill on west flank of Koeroegabvlakte, rounded shrublet in middle distance *Tylecodon hallii* (Tölken) Tölken (Crassulaceae). 21, *Masarina tylecodoni* Gess entering flower of *T. hallii.*

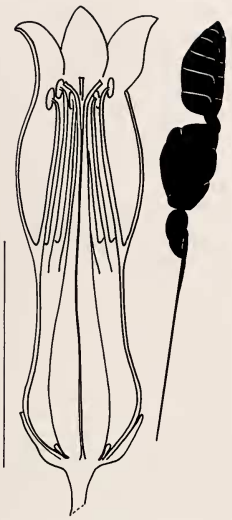


Fig. 22. Diagrammatic representations of half flower of *Tylecodon hallii* (Tölken) Tölken (Crassulaceae) cut longitudinally and of *Masarina codoni* Gess (wings and legs omitted).

Masarina tylecodoni, when visiting a flower for nectar, alights on the outwardly curved petal lobes and enters between the corolla and the filaments of the stamens which being closely adpressed form a barrier to the wasp which inserts its tongue between two filaments to reach the nectar at the base of the flower. In forcing its way into a flower the wasp pushes against the anthers and therefore when the anthers are ripe the wasp receives a load of pollen dorsally. When visiting a flower to collect pollen a wasp alights on the outwardly curved corolla lobes and standing thus ingests the pollen directly from the anthers.

Masarina tylecodoni should be considered as a potential pollinator of *T. hallii*. When coming from imbibing nectar from a flower in the pollen presenting phase and entering a flower with receptive stigmas which are outwardly curved it would effectively wipe off pollen from its dorsum onto one or more of the stigmas. If it is indeed dependant solely on *Tylecodon* for pollen and nectar, even if it visits more than one species of *Tylecodon*, it would be a dependable potential pollinator as *T. hallii* is the earliest of the *Tylecodon* species to come into flower in the Richtersveld.

DISCUSSION

Flower visiting.—The association between *Jugurtia codoni* and *Codon* is the first record of an association between a southern African masarine and Hydrophyllaceae, however, the Nearctic masarine genus *Pseudomasaris* shows a strong preference for flowers of this family. Flower visiting records are available for 13 of the *ca.* 15 described species of *Pseudomasaris* and of these 92% have been recorded from the genera *Phacelia* Juss. and *Eriodyction* Benth. (Gess, S.K. 1996).

The preference shown by *Masarina tylecodoni* for *Tylecodon* (Crassulaceae) is of interest as the only other record of a masarine visiting a species of Crassulaceae is that for *Celonites wahlenbergiae* Gess, which is primarily associated with *Wahlenbergia* (Campanulaceae), but has been recorded in addition from plants of several other genera and families, including *Crassula dichotoma* L. (Crassulaceae) (Gess and Gess 1992). The association with Crassulaceae (Rosales) is not so surprising if one considers that Rosales is considered to be basal in the Rosidae which includes the Fabales and therefore Papilionaceae with which are associated at least two species of *Masarina*.

That the flowers of *Zygophyllum* spp. (Rosidae: Sapindales: Zygophyllaceae) in the Richtersveld are visited, although apparently not favoured, by *Ceramius brevitarsis*, two species of *Jugurtia*, *J. codoni* and

J. koeroegabensis, and *Masarina mixtoides* is of interest. Although the Gesses have sampled *Zygophyllum* species in other areas where masarines have been present they have not encountered them visiting these flowers. The only other records of masarines visiting *Zygophyllum* are for a species of *Quartinioides* from *Zygophyllum simplex* L. at Gobabeb (23.34S, 15.03E) in the central Namib Desert (Wharton 1980). Indeed the only other record of a masarine visiting flowers of Zygophyllaceae seems to be that to *Larrea* Cav. by *Pseudomasaris wheeleri* Bequaert, a Nearctic species more typically associated with Scrophulariaceae, Hydrophyllaceae and Asteraceae (Richards 1966).

The association of *Masarina strucki* with *Hermannia* (Dilleniidae: Malvales: Sterculiaceae) is the first recorded association of a masarine with Sterculiaceae. Indeed an association with a member of the Dilleniidae as a whole is unusual for the Masarinae worldwide. Of the 164 other species of masarines for which flower visiting records are available only 13 have been recorded from Dilleniidae and most of these are species which are generally closely associated with plants of other classes so that the visits to Dilleniidae are casual in nature. Classes most favoured are Asteridae 104 species, Caryophyllidae 52 species (47 being from southern Africa), and Rosidae 41 species. Visits to other classes are for 3 species to Magnoliidae, 2 species to Liliidae and 1 species to Zingiberidae (classes *sensu* Cronquist 1988).

When taking into account the form of the flowers visited by southern African species it is of note that a masarine visiting the flowers of the favoured families Aizoaceae, Asteraceae, Campanulaceae, Scrophulariaceae and Papilionaceae is immediately in position for reaching the nectar and pollen supplies (Fig. 23 a–g). The same holds true for the erect campanulate flowers of *T. hallii* (Crassulaceae) and *C. royenii* (Hydrophyllaceae). By contrast when *M. strucki* alights on the outside of the downwardly directed bell flower of *Hermannia* it is not immediately in position for reaching these resources but must move down, pass around the lip of the corolla, and then turn upwards to be positioned for reaching them (Fig. 23h).

Discussion of nesting.—The nesting of *M. strucki* is remarkably different from that of *M. familiaris* the only other *Masarina* for which nesting has been recorded (Gess and Gess 1988) and from the nests known for the closely related genus *Jugurtia*, that is those of *J. confusa* Richards (Gess and Gess 1980) and *J. braunsi* (Schulthess) (Gess, S.K. 1996).

In nest construction *M. strucki* unlike the other three species apparently excavates the burrow without the use of water and does not construct an entrance turret. Excavation of a nest with the use of water and the construction of a turret are considered to be basal for the masarines, and excavation without the use of water and without the construction of an entrance turret to be derived (Gess, S.K. 1996). Such a change has occurred independantly several times having been recorded for two species of *Rolandia* (Gess *et al.* 1995 and Houston 1995), and for *Celonites latitarsis* Gess (Gess and Gess 1992). Excavation of the nest without the use of water has also been recorded for *Quartinia vagepunctata* Schulthess (Gess and Gess 1992), however, this species does construct a turret but using self-generated silk not water as a bonding agent.

The cell of *M. strucki* like that of *Masarina familiaris* is an excavated cell with the walls impregnated with a bonding substance unlike those of the two *Jugurtia* species, in which distinct earthen cells are constructed within excavated cells. However, the bonding substance used by *M. strucki* is apparently nectar whereas that used by *M. familiaris* is water. Furthermore, the cells of the two *Masarina* species differ in shape. The cell of *M. strucki* has the inner end rounded like those of all other masarines for which cells are known

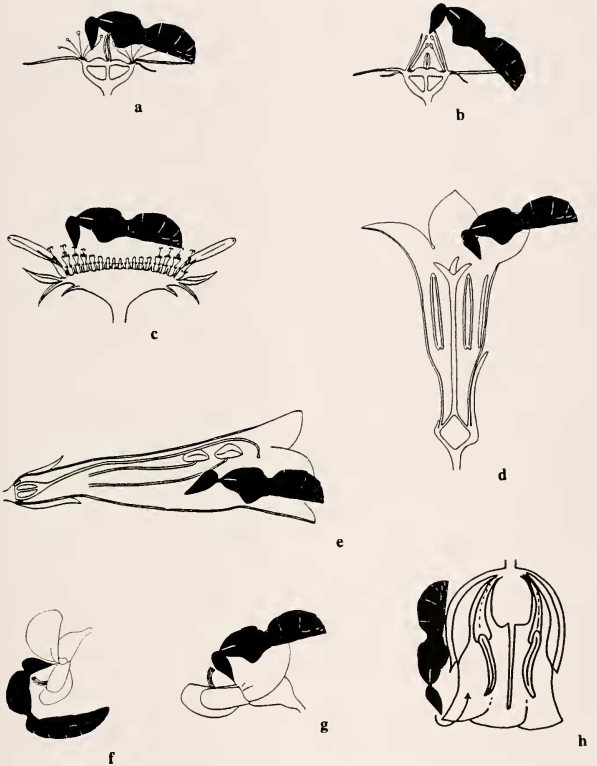


Fig. 23. Diagrammatic representations to show how masarines position themselves when preparing to utilize flowers of the types visited by them. a, Stamen carpet flower (Aizoaceae: Mesembryanthema). b, Cone flower ((Aizoaceae: Mesembryanthema). c, Capitulum (Asteraceae). d, Campanulate flower (Campanulaceae). e, Gullet flower (Scrophulariaceae). f and g, Papilionate flower (Papilionaceae). h, Bell flower (Sterculiaceae).

other than that of *M. familiaris* which is distinctly truncate (Gess, S. K. 1996). The use of nectar as a bonding agent has been recorded for *Pseudomasaris* (Torchio 1970) and suggested for *Celonites* (Gess and Gess 1992).

That *M. strucki* lays the egg free from the cell wall is usual for ground nesting masarines. In this *M. strucki* again differs from *M. familiaris* which, like the aerial nesting *Gayella eumenoides* Spinola (Claude-Joseph 1930) and *Pseudomasaris edwardsi* (Cresson) (Torchio 1970), attaches the egg to the cell wall.

The preparation of a very moist provision mass is common to both *M. strucki* and *M. familiaris*. In this they differ from *J. confusa* which prepares a firm provision mass. The construction of papillae seems to be a recurring feature of very moist pollen masses having been recorded also for that of *Pseudomasaris edwardsii* (Cresson) (Torchio 1970) but not for the less moist pollen masses of *Pseudomasaris maculifrons* (Fox) (Parker 1967) and *Pseudomasaris phaceliae* Rohwer (Parker 1967 and Torchio 1970) and in the present paper for *Celonites gariepensis*.

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